VARIANCE AND COVARIANCE COMPONENT ESTIMATION OF REPRODUCTIVE TRAITS IN A MULTIBREED BEEF CATTLE HERD APPLYING LINEAR AND THRESHOLD MODELS

BY

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(Animal Science)

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"*Declaration*

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

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ABSTRACT

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The main object of this study was to estimate heritabilities and possible genetic correlations for and between reproductive traits in a composite multibreed beef cattle herd. Reproduction is a complex process with many components. Due to the nature of the data, obtained from the two farms of the Johannesburg Metropolitan Council from 1974 to 1993, only calving date (CD), calving date with a penalty score (CDP), calving success (CS), calving interval (CI), age at first calving (AFC), longevity and stayability at 36, 48, 60, 72 and 84 months were investigated.

A GFCAT set of programmes was used and fitted on a sire model to analyse all the categorical traits. Heritabilities and product moment correlations between predicted breeding values for stayability at 36, 48, 60, 72, 84 months, calving success (CS) and longevity, were estimated. The estimated heritabilities on the underlying scale for these traits were 0.06, 0.10, 0.06, 0.03, 0.11, 0.03 and 0.08, respectively. Product moment correlations between breeding values for stayability traits were very low. The highest correlation of 0.22 was obtained between 36 and 48 months. Heritability estimates and correlations between traits appear to be of such a low magnitude that selection for these characteristics would result in limited improvement and indicate that the sire had little influence on his daughter's stayability, longevity and CS.

For the analyses of linear traits (CI, CD, CDP and AFC), a REML procedure fitting a multitrait animal model (using REML VCE 4.2.5 package of Groeneveld, 1998) was used. Heritabilities and genetic

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correlations for and between calving interval (CI), calving date (CD), calving date with a penalty score (CDP) and age at first calving (AFC) were estimated as traits of the dam. The estimated heritabilities for CI, CD, CDP and AFC obtained in this study were 0.01, 0.04, 0.06 and 0.40, respectively with a repeatability of 0.07, 0.12 and 0.13 for CI, CD and CDP, respectively. Genetic correlations between traits obtained varied from low to moderate, except for the high correlations between CD and CDP (0.98), CI and CD (0.75) and CI and CDP (0.79). Heritabilities, genetic correlations and repeatabilities of CD and CDP obtained in this study suggest that CD and CDP are the same traits and that selection for CDP rather than for CD does not have any additional advantage. Due to the additional advantages of CD over CI and the fact that CD is a less biased measurement of the female reproductive complex, CD appears to be of genetic value and should be considered as a possible selection criterion to ensure genetic improvement for reproduction in a beef cattle herd.

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OPSOMMING

BERAMING VAN VARIANSIE EN KO-VARIANSIE KOMPONENTE VAN REPRODUKSIEKENMERKE IN 'N MEERRAS VLEISBEESKUDDE DEUR MIDDEL VAN LINEÊRE EN DRUMPEL WAARDE MODELLE

deur

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Die doel met hierdie studie was om oorerflikhede vir en moontlike genetiese korrelasies tussen verskillende reproduksiekenmerke in 'n meerras vleisbeeskudde te bepaal. Reproduksie is 'n komplekse proses en bestaan uit veelvuldige komponente. Weens die aard van die data, verkry vanaf die Johannesburg Metropolitaanse Raad se twee plase (vanaf 1974 tot 1993), is slegs kalfdatum (CD), kalf datum met 'n verswaringswaarde (CDP), kalwingsukses (CS), kalfinterval (CI), ouderdom met eerste kalwing (AFC), langlewendheid en volhoubaarheid van die moeders om reproduktief in die kudde tot op onderskeidelik 36, 48, 60, 72 en 84 maande te bly, bestudeer.

Kategoriese kenmerke is deur middel van 'n GFCAT stel programme, wat op 'n vadermodel gepas is, geanaliseer. Oorerflikhede vir en die produkmoment korrelasies tussen die voorspelde teelwaardes vir CS, langlewendheid en volhoubaarheid op onderskeidelik 36, 48, 60, 72 en 84 maande, is bereken. Die oorerflikhede vir bogenoemde kenmerke was onderskeidelik 0.03, 0.08, 0.06, 0.10, 0.06, 0.03 en 0.11. Die korrelasie tussen die voorspelde teelwaardes vir die verskillende volhoubaarheidskenmerke was laag. Die hoogste korrelasie, nl. 0.22, is tussen 36 en 84 maande verkry. Die oorerflikhede en korrelasies tussen die kenmerke blyk van so 'n lae omvang te wees dat direkte seleksie vir die kenmerke slegs tot 'n beperkte genetiese verbetering sal lei en dui daarop dat die vader slegs 'n beperkte invloed op CS, volhoubaarheid en die langlewendheid van sy dogters het.

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Vir die analise van die lineêre kenmerke (CI, CD, CDP en AFC), is 'n REML-prosedure gebruik wat op 'n multikenmerk dieremodel gepas is (deur die gebruik van die REML VCE 4.2.5 pakket van Groeneveld, 1998). Oorerflikhede vir en genetiese korrelasies tussen CI, CD, CDP en AFC is bereken as kenmerke van die moeder. In hierdie studie is die beraamde oorerflikhede vir CI, CD, CDP en AFC as onderskeidelik 0.01, 0.04, 0.06 en 0.40 bepaal, met herhaalbaarhede van onderskeidelik 0.07, 0.12 en 0.13 vir CI, CD en CDP. Genetiese korrelasies tussen die kenmerke het van laag tot matig gevarieer, behalwe vir die hoë korrelasies tussen CD en CDP (0.98), CI en CD (0.75) en CI en CDP (0.79). Die oorerflikhede en herhaalbaarhede vir en genetiese korrelasie tussen CI en CDP verkry in hierdie studie, veronderstel dat CD en CDP in wese dieselfde kenmerk is en dat seleksie vir CDP in plaas van CD geen addisionele voordele inhou nie. Weens die addisionele voordele wat CD inhou, bo die van CI, en die feit dat CD 'n minder sydige bepaling van die vroulike reproduksiekompleks is, blyk CD van genetiese waarde te wees en moet dit as 'n moontlike seleksie kriterium, om genetiese verbetering in 'n vleisbeeskudde te verseker, oorweeg word.

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CHAPTER 1
GENERAL INTRODUCTION

Beef producers are faced with decreasing real returns since input prices increase without an associated increase in producer prices. This resulted in negative growth in terms of the real price of beef over the last few decades. To ensure the same level of return on investment, greater levels of efficiencies are required.

Reproduction is the most important factor influencing the economy of a beef production enterprise. Dickerson (1978) suggested that there is more potential for increasing both biological and economic efficiency in a herd through genetic improvement of reproduction than through changing either growth rate or body composition.

Although reproduction is of critical importance to overall efficiency in the livestock industry, a completely satisfactory measure of reproduction has not been found. Reproduction is a complex process consisting of many component traits. Several such components have been used as measures of reproductive performance. Calving interval (CI), calving rate, services per conception, age at first calving (AFC), calving date (CD), days to calving (DC) and calving success (CS) are some of the components of the female "reproductive complex" that have been considered as possible selection criteria by a number of animal geneticists.

Traditionally, CI was used to assess reproductive efficiency on the individual level. In general, heritability estimates for CI found in the literature are low. Koots *et al.* (1994) reported a mean heritability (h^2) of 0.01 for CI. Bourdon & Brinks (1983), Marshall *et al.* (1990) and MacGregor (1995) found CI to be a biased measure of reproductive performance due to its negative association with previous calving date (PCD). This results in cows calving early having the longest subsequent CI. Direct selection for a shorter CI could also result in indirect selection for later age at puberty, since cows with the shortest CI are often those that calved late in the previous calving season. For numerous reasons, Bourdon & Brinks (1983), Buddenberg *et al.* (1990), Lòpez de Torre & Brinks (1990), Marshall *et al.* (1990) and MacGregor (1995), suggested calving date as the preferred reproduction measurement applicable to a restricted breeding season.

The heritability estimates of all reproductive traits found in the literature are low and it appears that selection for these traits would result in limited genetic improvement (Hudson & Van Vleck, 1981; Van Doormaal *et al.*, 1986; López *de* Torre & Brinks, 1990; Koots *et al.,* 1994; Snelling *et*

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al., 1995). Higher heritability estimates were obtained in sheep when a threshold model was fitted (Snyman *et al.*, 1998). No comparable estimates were obtained in beef cattle. Selection for reproduction was neglected in the past due to these low heritabilities and other reasons, such as the difficulty in accurately measuring reproductive performance at an early age and the lack of suitable computer software (Olivier *et al.*, 1998). Harwin *et al.* (1967) reported in the sixties that the average national calving percentage in beef herds in South Africa did not exceed 55-60 %. Likewise, Meaker (1984) reported an average of less than 60 %. Veterinary reports of 1996, obtained from the National Department of Agriculture, indicate that the national calving percentage is still below 60 % (MacGregor, 1997). It therefore appears that, despite the change from subjective selection of cattle to objective selection based on economically important traits, no significant change in calving percentage has taken place over the past thirty years.

Livestock have to both reproduce regularly and stay alive to be of any economic interest to the breeder. Animals are most likely to be culled as a result of poor production and reproduction. The average lifespan of livestock is far below their biological potential and disposal due to old age are rare. Therefore fitness is also of great interest. Charles Darwin (1859) introduced fitness as the characteristic by which individuals of a genetically heterogeneous population, that are in competition for limited resources, are selected through natural selection. With this definition, characteristics are classified in major components of fitness (for example number of parities, litter size and survival of progeny), characteristics with an intermediate optimum for fitness (for example body size and milk yield in mammals) and fitness neutral characteristics (for example number of abdominal bristles in *Drosophila*). Due to the long preceding period of natural selection, longevity (number of parities) and other fitness-related traits should have been very close to optimal before the beginning of artificial selection in livestock populations. In animal breeding, however, selection is mainly aimed at characteristics that increase production with an intermediate optimum for fitness in a Darwinian sense. As a consequence, artificial selection should generally lead to a deterioration of longevity if this criterion is not sufficiently considered in the selection process (Essl, 1998).

Gowe (1983) suggested that heritabilities of reproductive traits are non-linear due to directional dominance and recessive deleterious mutations, with heritabilities being higher on the lower fitness side. Hence, slight culling on low reproductive fitness should already be effective in preventing the usually observed decline in reproductive performance when the main selection pressure is on other traits. This hypothesis was confirmed in selection experiments of Frankham *et al.* (1988) and Gowe (1983).

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Although natural selection among artificially selected individuals still exists to some extent, most of the theoretical framework of quantitative genetics in animal breeding relies on the simplified assumption that natural selection is absent (Falconer, 1981). This simplification may, however, lead to discrepancies between the expected and realized response to artificial selection (Essl, 1998).

All individual fitness characteristics are simultaneously partial determinants of longevity. Therefore, longevity includes the whole fitness complex to a great extent (Essl, 1998). The lifespan of a female animal is often partitioned into two time periods. Firstly, the costly period from birth to first parity and secondly, the following productive period until disposal. This second period, rather than the whole lifespan, is generally called longevity (Essl, 1998). However, more distinct terms such as length of productive life, herd life or number of parities are also used for the productive period.

The capability of a reproducing animal to be retained in the herd over time is often called stayability or survival. The term stayability is also used as a measurement of the fraction of animals which are still alive at a particular age (for example age of 48 months for cows) within a so-called "opportunity group" (for example a group of animals with the opportunity to live 48 months).

Some of the reproductive traits such as calving success, longevity and stayability manifest themselves as threshold traits, while other components such as calving date, calving interval, age at first calving (in days) are continuous rather than of a threshold nature. In this study, calving success, longevity, stayability, calving interval, calving date and age at first calving were under investigation. Due to the nature of the data, no other traits were considered.

Heritability estimates for all of the continuous traits (calving interval, calving date and age at first calving) were obtained by using a restricted maximum likelihood procedure while heritability estimates for all categorical traits (calving success, longevity and stayability levels) were obtained by using threshold analysis. Most studies that were carried out in the past were based on unitrait analysis. This was most likely due to the lack of suitable computer software to run multitrait analyses. Suitable computer software now exists to run multitrait analyses on linear traits. In this study all linear traits were analysed by using multitrait analysis. The advantage of using multitrait analysis is that it is possible to obtain genetic correlations between traits. Heritability estimates

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will also be predicted more accurately because of the inclusion of the genetic correlations between traits in the model and valuable information can be obtained in this way.

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CHAPTER 2

HERITABILITY ESTIMATES OF REPRODUCTION AND STAYABILITY TRAITS IN A BEEF CATTLE HERD USING THRESHOLD ANALYSIS

2.1 Introduction

Breeding goals normally differ according to the environment and production system. However, survival and reproduction is of utmost importance in any environment and under any production system.

Efficient production in any species depends on the production of females, mostly her reproduction and the growth of her progeny (Dickerson, 1970). For a commercial cow/calf producer whose primary goal is to produce a live, healthy calf annually, no factor plays a more vital role than the reproductive fitness of the female. Dickerson (1978) suggested that there is more potential for increasing both biological and economic efficiency in a herd through genetic improvement in reproduction than through either changing growth rate or body composition. Doyle *et al.* (2000) also reported that, at the commercial level, reproduction was ten times as important as growth and twenty times greater than end-product attributes. Melton (1995) reported that the theoretical relative economic value of reproduction was 3.24 times greater than that of consumption attributes. All of these authors strongly emphasise the importance of reproduction to productivity at the commercial cow/calf level.

Reproduction is a complex process with many components, especially in female reproduction. Some of these components, such as calving success, longevity and stayability manifest themselves as threshold traits, while other components such as calving date, calving interval, age at first calving (in days) etc. are continuous rather than of a threshold nature. Threshold traits are not continuous in their expression, but exhibit distinct categorical phenotypes. The understanding of the inheritance of such traits lies in the visualisation that the trait has an underlying continuity with a threshold, which imposes a discontinuity on the visible expression of the trait (Falconer & Mackay, 1996). The relationship between polygenes and the expression of discontinuous traits comes about through the establishment of thresholds.

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Improving reproductive performance depends on the reproductive fitness of replacement heifers and cows in the female herd. Due to the large investment of time and resources associated with replacement heifer development, much of the success of an operation, in a favourable environment, depends on getting heifers to calve at two years of age. They must then be subsequently kept in the herd long enough to produce a minimum number of calves to cover their own expenses as well as a share of those expenses associated with cows that fall out of the herd early in their production life. Therefore, it is important to select those heifers with higher genetic potential for fertility that will breed early in their first calving season and continue to breed and calve early every year as mature females (Doyle *et al.*, 2000).

The average lifespan of livestock is mostly far below their biological potential and disposal due to old age are rare. The lifespan of a female animal is often partitioned into two time periods, firstly the costly period from birth to first parity and secondly, the following productive period until disposal. This second period, rather than the whole lifespan, is generally called longevity (Essl, 1998).

The capability of an animal to remain in the herd over time is often called stayability. The term stayability is also used as a measurement of the fraction of animals which are still alive at a particular age (for example 48 months of age) within a so-called "opportunity group" (for example a group of animals with the opportunity to live up to 48 months of age). Although the observation (either 0 or 1) is recorded on the individual, this characteristic is essentially restricted to the evaluation of sires. Hudson & Van Vleck (1981) defined stayability as the probability of surviving to a specific age, given the opportunity to reach that age. Snelling *et al.* (1995) defined stayability as the probability of a cow in production raising a calf after reaching her breakeven age.

The meaning of stayability traits can change, depending on the age considered and which animals are considered to have the opportunity to reach a specific age, given the opportunity to reach that age. For beef cows, a useful stayability trait is the probability that a cow in production will remain in production to raise enough calves to pay for her development and maintenance cost. The age a cow must reach to breakeven depends on the value of replacement females, annual profit per cow and salvage value of culled cows (Dalsted & Guiterrez, 1989). As shown by Dalsted & Guiterrez (1989), a cow must remain in the herd for one to fourteen years to reach her breakeven point, depending on the environment and economic conditions. Favourable economic conditions may allow a cow to pay for herself within three or fewer calves, while more typical situations demand that a cow produce at least five calves. For a herd to be profitable, some cows must remain in

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production past their breakeven number of calves to compensate for the cost of those cows that were culled before their breakeven age.

Unfortunately selection for reproduction was neglected in the past. This was due to various reasons, such as the difficulty in accurately measuring reproductive performance at an early age, the low heritabilities for reproduction traits, as reviewed by Koots *et al.* (1994), and the lack of suitable computer software to estimate variance components and predict breeding values for these traits (Olivier *et al.*, 1998). This is especially true for extensive beef cattle production. The recent availability of appropriate statistical software and computer hardware have made it possible to obtain more accurate estimates of genetic parameters and breeding values for reproductive traits.

In the past linear model methodology, such as Henderson's method III, was most frequently used for the analysis of discontinuous as well as continuous data (Olivier *et al.* 1998). The problem when analysing discontinuous data with linear procedures, is that the method of analysis is based on continuous phenotypic distributions and does not take the discontinuity of threshold traits into consideration. Gianola (1982) stated that the main theoretical reason for not using BLUP (best linear unbiased prediction) with categorical data is that breeding values and residuals are not independent of one another. Threshold procedures should therefore be more suitable when analysing reproduction and stayability traits, which have definite categorical characteristics.

The objectives of this study were to employ threshold procedures to estimate heritabilities and possible correlations between the predicted sire breeding values of stayability at 36, 48, 60, 72 and 84 months, longevity and calving success.

2.2 Materials and Methods

2.2.1 Data description

Data for this study were obtained from a multibreed composite beef cattle herd of the Johannesburg Metropolitan Council. The animals were kept on two farms on an intensive management system (Paterson, 1981; MacGregor, 1997). Animals were mainly bred during two restricted breeding seasons of approximately three to four months. They were bred, using AI, during September to December each year to calve from June to September the following year. Animals which did not conceive during this breeding period, were rebred from May to July.

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Records of heifers and cows in production from 1974 until 1993 were included in the analysis. However, incomplete records and data of those who calved outside these two restricted calving seasons were removed from the dataset.

During this period 5 694 heifers entered the herd. 78% of these heifers were not culled at 36 months of age, while 56% were still in the herd at 48, 38% at 60, 27% at 72 and 19% at 84 months of age (Fig. 2.1).

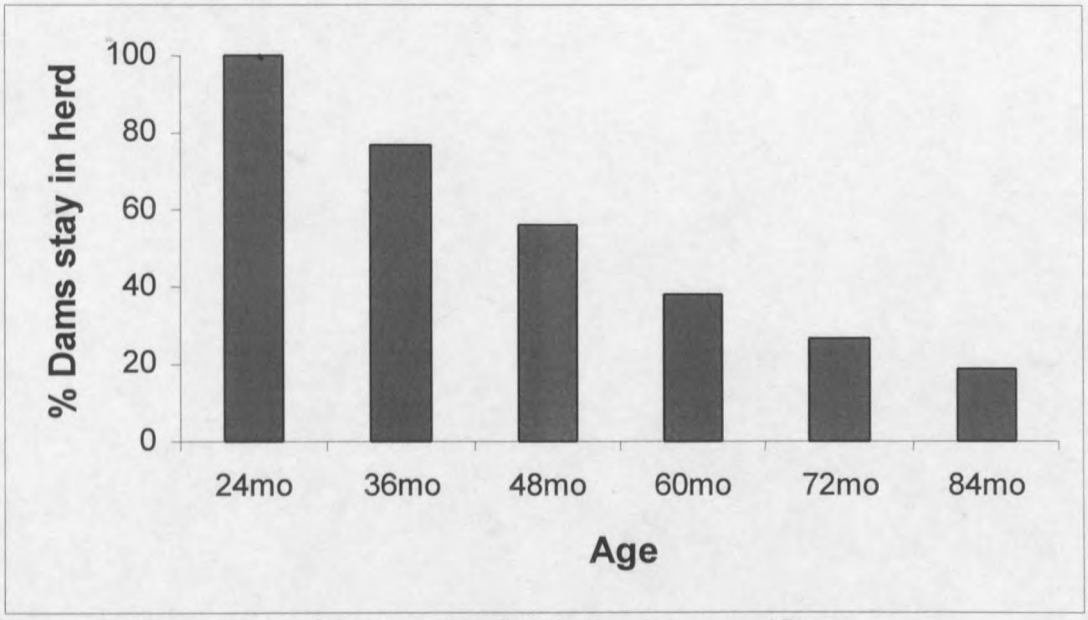

Figure 2.1 Percentage of dams retained in the herd at a specific age compared to 24 months of age

Of all females present at 24 months of age, 76% were retained at 36 months of age, while 24% were culled. Of those culled, the majority was due to their failure to calf (22 %) while only a few (2%) were culled despite the fact that they had calved. Reasons for culling of these females were not recorded. Of all the females that survived culling at 36 months of age, 80% were retained at 48 months of age, while 20% were culled. Once again, the majority was culled due to their failure to calve (19%). Seventy nine percent of all the females that were retained in the herd at 72 months and survived to 84 months of age were not culled at 84 months of age, while 21% of them were culled. Sixteen percent of these females were culled due to their failure to calve while 5% were culled despite the fact that they had calved. Table 2.1 presents these figures for all the stayability levels. There was no evidence that more cows were culled at different stayability levels.

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Throughout all five stayability levels, between 20 and 24% of the females that reached that specific age, were culled.

Table 2.1 Percentage of animals that were retained or were culled for each of the stayability levels according to their reproduction success

	Stayability levels									
	36 months		48 months		60 months		72 months		84 months	
	Retain	Cull	Retain	Cull	Retain	Cull	Retain	Cull	Retain	Cull
Did calve	70	2	74	1	74	3	75	4	74	5
Did not calve	6	22	6	19	4	19	5	16	5	16
TOTAL	76	24	80	20	78	22	80	20	79	21

2.2.2 Trait description

The traits included in the study were calving success, stayability at different age levels (36, 48, 60, 72 and 84 months) and longevity.

Stayability was defined as the probability of an animal surviving to a specific age, given the opportunity to reach that age. For the stayability levels the data was divided into five opportunity groups, each including only records of animals having the opportunity to survive to 36, 48, 60, 72 and 84 months. The record of an animal in any particular opportunity group was also logically included in earlier opportunity groups since it is a closed herd with no females coming from outside. Stayability records were thus coded as either 1 if the cow survived to the given age, or 0 if it was her last recorded record. This is because of the fact that she was culled at this stayability level and did not survive to the next level. Stayability was measured each year for each of the different opportunity groups.

Calving success was also coded with either 1 or 0. If a cow had calved during that specific year, she was assigned 1, otherwise 0. Longevity was calculated as the age at which the cow had her last record. For example, if a cow had her last record at 6 years of age, she was assigned a longevity record of 6. Longevity varied between two and ten years (ten year longevity also included dams older than ten years) and therefore had nine categories.

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The dataset contained 5 694 daughters of 243 sires that were in the herd at 36 months of age (Table 2.2). These values decreased as the age of the daughters increased. Therefore, only 1 366 daughters of 128 sires were still in the herd at 84 months age.

During the period of investigation, 5 808 daughters of 171 sires were culled or died. Longevity was therefore evaluated on 5 808 daughter records of 171 sires (Table 2.2).

Table 2.2 Number of sires and records used in this study for each of the traits

	Calving success	Stayability levels					Longevity
		36 mo	48 mo	60 mo	72 mo	84 mo	
Number of sires	254	243	220	178	146	128	171
Number of daughters	26 177	5 694	3 972	2 775	1 900	1 366	5 808

2.2.3 Sources of non-genetic variation

In order to determine the importance of the possible contribution of non-genetic sources of variation on the traits, the categorical data modelling "CATMOD", procedure of the SAS Institute Inc. (1993), was used. Farm, dam age, calving success (applied only to longevity and stayability levels), the dam's birth year and the production year were considered as non-genetic sources of variation in the initial model. All non-genetic sources were treated as fixed effects. Table 2.3 presents the number of levels for each fixed non-genetic effect applied to each trait in the final model. Two models were used for the analysis of the five stayability levels rather than one. For the first model, farm, calving success and the dam's birth year were included as fixed effects, while model two included farm, calving success and production year as fixed effects. Production and birth year are both of biological value, but the model became overspecified when both were included. Therefore, two models were used.

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Table 2.3 Number of levels of each fixed non-genetic effect

Non-genetic sources	Calving success	Stayability levels					Longevity
		36 mo	48 mo	60 mo	72 mo	84 mo	
Farm		2	2	2	2	2	2
Dam age	9						
Calving success		2	2	2	2	2	2
Dam birth year	19	19	18	17	15	15	18
or							
Production year	19	18	19	18	15	16	

2.2.4 Threshold model analysis

Since threshold traits are not normally distributed, but expressed in two or more distinct categories, a threshold model was used to estimate heritabilities and to predict breeding values. A set of programmes (GFCAT), for the analysis of "mixed" threshold models, based on the principles described by Gianola & Foulley (1983) and developed by Konstantinov (1995) was used. These non-linear methods are based on the standardised threshold model concept, under which the trait occurs as a result of an underlying unobserved phenotype exceeding a threshold (Konstantinov *et al.*, 1994). The unobserved continuous phenotypes are assumed to be normally distributed.

The following model was used:

$$\mu = X\boldsymbol{b} + Z\boldsymbol{s}$$

where

μ is a vector of underlying means,
$\boldsymbol{b}$ is a vector associated with the fixed effects,
$\boldsymbol{s}$ is a vector of sire effects and
X and Z are design matrixes.

Solutions for thresholds and values for b and s were computed as described by Konstantinov *et al.* (1994).

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Since this is a sire model and the procedure used requires that the sire variance (σ_s^2) be known, a REML-type procedure, proposed by Harville & Mee (1984), was used.

Heritabilities (h^2) were estimated as:

$$h^2 = \frac{4\sigma_s^2}{(1+\sigma_s^2)}$$

To obtain an indication of the genetic correlations between traits, simple product moment correlations between the predicted breeding values of the individual sires were estimated for each trait.

2.3 Results and Discussion

2.3.1 Contribution of non-genetic sources

The significance levels for each non-genetic effect for each level of stayability, calving success and longevity are presented in Table 2.4.

Farm, calving success, the dam's birth year and the year in which the dam had a record for that specific level (production year) were significant ($P \leq 0.01$) for stayability at 36, 48, 60, 72 and 84 months. Farm was not significant ($P = 0.125$) for calving success, therefore only dam age, the dam's birth year and production year were included as fixed effects in the operational model. Farm, calving success and the dam's birth year were significant ($P \leq 0.01$) for longevity and were therefore included as fixed effects in the operational model.

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Table 2.4 Levels of significance of non-genetic sources for stayability levels, calving success and longevity

Trait	Farm	Calving success	Dam age	Dam birth year	Production year
36 mo (model 1)	0.0018	0.0001		0.0001	
36 mo (model 2)	0.0018	0.0001			0.0001
48 mo (model 1)	0.0012	0.0001		0.0001	
48 mo (model 2)	0.0012	0.0001			0.0001
60 mo (model 1)	0.0016	0.0001		0.0001	
60 mo (model 2)	0.0016	0.0001			0.0001
72 mo (model 1)	0.0025	0.0001		0.0001	
72 mo (model 2)	0.0025	0.0001			0.0001
84 mo (model 1)	0.0035	0.0001		0.0001	
84 mo (model 2)	0.0035	0.0001			0.0001
Calving success	0.1250		0.0001	0.0002	0.0001
Longevity	0.0100	0.0010		0.0001	

Table 2.5 shows the percentage of dams retained in the herd for farm, calving success and also for the dam's birth and production year at the 36, 48, 60, 72 and 84 months stayability levels. In general, a higher percentage of dams were retained on farm one than on farm two, except for the 72 months stayability level where 80.9% of the dams that reached 72 months of age were retained in the herd in comparison to the 82.3% of dams on farm two. For the 36 months opportunity group, 98.8% of the dams that did calve during the period of investigation were retained in the herd while 22.8% of the dams that did not calve were retained. This clearly illustrates that culling at different levels was mainly due to failure to calve in the previous year. In 1984, for stayability at 36 months, 54% of the dams were retained leaving 46% that were culled. In 1977, only 15% of the dams that reached 36 months of age were culled, therefore 85% of them were retained in the herd for this particular year. The percentage of dams culled each year differ between years. Therefore, the dam's birth year was additionally included as a non-genetic effect in the operational model.

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Table 2.5 The percentage of dams retained in the herd at 36, 48, 60, 72 and 84 months of age for farm, calving success and for each dam's birth and production year.

Non-genetic Effects	Levels	Stayability levels				
		36 months	48 months	60 months	72 months	84 months
Farm						
	1	78.37	80.87	80.54	80.88	82.07
	2	76.02	78.75	78.27	82.30	81.58
Calving success						
	Calve	98.84	98.76	97.68	97.29	95.83
	Did not calve	22.83	22.52	19.37	22.74	28.52
Dam's birth year						
	1973	54.86	73.74	74.07	74.47	75.86
	1974	85.44	69.47	85.12	68.42	79.63
	1975	70.37	76.47	72.86	76.47	66.67
	1976	77.14	68.94	80.91	79.31	80.56
	1977	73.54	78.95	75.84	78.07	70.33
	1978	65.87	70.64	69.62	73.08	69.05
	1979	72.33	77.69	65.59	77.01	83.33
	1980	64.54	67.03	71.20	82.02	84.29
	1981	53.71	72.04	85.29	85.96	87.76
	1982	70.11	80.00	90.20	85.26	82.72
	1983	80.28	83.56	83.33	81.13	88.00
	1984	84.30	81.76	80.59	87.27	85.64
	1985	79.35	86.36	84.59	87.28	77.38
	1986	81.65	86.71	83.33	80.09	90.29
	1987	84.33	81.22	71.96	85.24	73.33
	1988	79.18	78.51	87.72	72.73	
	1989	81.10	87.53	78.26		
	1990	84.93	71.76			
	1991	76.06				
Production year						
	1975	43.33				
	1976	63.10	61.54			
	1977	85.44	78.08	81.25		
	1978	70.37	69.47	71.05	61.54	
	1979	77.14	76.47	85.12	79.41	77.78
	1980	73.54	68.94	72.86	68.42	75.00
	1981	65.87	78.95	80.91	76.47	79.63
	1982	72.33	70.64	75.84	79.31	66.67
	1983	64.54	77.69	69.62	78.07	80.56
	1984	53.71	67.03	65.59	73.08	70.33
	1985	70.11	72.04	71.20	77.01	69.05
	1986	80.28	80.00	85.29	82.02	83.33
	1987	84.30	83.56	90.20	85.96	84.29
	1988	79.35	81.79	83.33	85.26	87.76
	1989	81.65	86.36	80.59	81.13	82.72
	1990	84.33	86.71	84.59	87.27	88.00
	1991	79.18	81.22	83.33	87.28	85.64
	1992	81.10	78.51	71.96	80.09	77.38
	1993	84.93	87.53	87.72	85.24	90.29
	1994	76.60	71.76	78.26	72.73	73.33

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There is a three-year time lag between birth year and production year. In other words, dams that were 36 months of age in 1984 were born in 1981 and therefore production year and the dam birth year will be of the same pattern. The only difference between the two effects will be the year number. For example, for 36 months stayability, the difference will be three years between the dam's birth year and production year, four years for 48 months stayability and seven years for 84 months stayability. The pattern, therefore, remains the same. Therefore, if either of them was significant, the other one should also be significant. The best production years (the year in which the dams calved), where the least number of females were culled, were 1993, 1993, 1991 and 1993 for 48, 60, 72 and 84 months stayability, respectively. These were the females that were born in 1989, 1988, 1985 and 1986, and were also the dams that were the least culled for 48, 60, 72 and 84 months stayability, respectively (Table 2.5).

Figure 2.2 shows the percentage of dams that calved each year from 1974 to 1993 and also the percentage of dams that calved within their birth year group. The cows born in 1985 were the most productive dams, having an average of 77 % calvings per calving opportunity, while those born in 1973 were the least productive with only 61 % calvings per calving opportunity. Of all the cows that were in production in 1975 only 44 % calved, while 78 % of the cows that were in production calved during 1990.

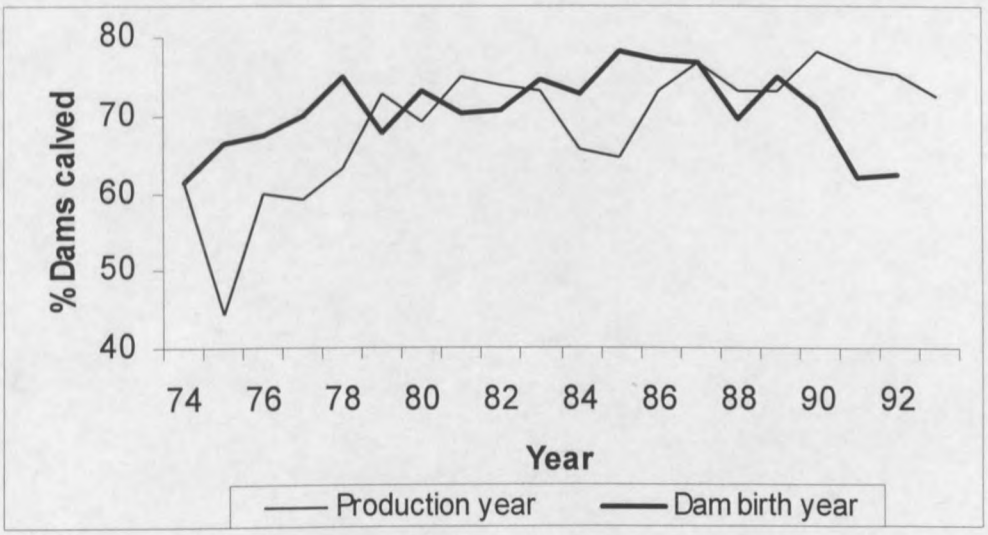

Figure 2.2 The percentage of dams calved for the dams birth year and production year

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Unfortunately, the model became overspecified when both the dam's birth year and the year the dam had a record for a specific trait (production year) were included. Both of them, however, were significant and are of biological value. A dam could for instance have been born during a dry year, which could cause poor reproductive development, and would thus most likely have been culled at an earlier age. The same applies for production year. A bad year could therefore influence a cow considerably and may result in a cow being culled as a result.

2.3.2 Threshold solutions

Solutions for thresholds, farm, calving success (CS) and dam age are presented in Table 2.6. Only two categories (one threshold) were used for stayability and calving success, while longevity had ten categories (nine thresholds). The thresholds are given as a deviation from the first threshold, which is set to zero. Table 2.6 shows an increase in the threshold for longevity with a subsequent drop after threshold eight, which is the threshold between nine and ten years of age. This emphasises that a dam's chances to stay in the herd increased as her age increased until nine years of age, after which it dropped rapidly, probably owing to the practice of culling for age.

The solutions obtained for farm, calving success and dam age are all deviations from the last category, which is set to zero. Across all stayability levels, animals on farm two had a higher probability to be retained in the herd.

The solutions for dam age, as a fixed effect for calving success, varied over the various age levels, and it is evident that no distinct pattern exists. However, eight-year-old dams had a higher probability to give birth to a calf, while the two-year-olds were more likely to fail.

For the purpose of discussing threshold solutions, the solutions for the dam's birth year and production year have no biological value. They were therefore, not presented or discussed in this paper.

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Table 2.6 Solutions for thresholds, farm, calving success (CS) and dam age

	Stayability										CS	Longevity
Months	36		48		60		72		84			
Model	1	2	1	2	1	2	1	2	1	2		
Thresholds												
1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
2												0.5713
3												0.9440
4												1.2788
5												1.5363
6												1.7642
7												2.0104
8												2.2216
9												0.2843
Farm												
1	-0.3270	-0.3339	-0.2406	-0.2449	-0.1212	-0.1282	-0.1337	-0.1337	-0.0239	-0.0263		
2	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		
CS												
1	-3.4659	-3.4641	-3.2755	-3.3192	-2.8833	-2.9154	-2.5786	-2.5786	-2.3625	-2.3720		0.7163
2	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
Dam age												
2											-0.4573	
3											0.1249	
4											0.3587	
5											-0.2710	
6											-0.3649	
7											-0.2948	
8											0.6426	
9											-0.1837	
10											0.0000	

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2.3.3 Heritability estimates

The heritability estimates for each trait are given in Table 2.7. The heritabilities for the different stayability levels are in close agreement for both models, therefore, only the results from Model 1 are discussed.

Table 2.7 Heritabilities of reproductive and stayability traits

Trait		Heritability
Calving Success		0.03
36 month stayability	Model 1	0.06
	Model 2	0.04
48 month stayability	Model 1	0.10
	Model 2	0.07
60 month stayability	Model 1	0.06
	Model 2	0.05
72 month stayability	Model 1	0.03
	Model 2	0.03
84 month stayability	Model 1	0.11
	Model 2	0.11
Longevity		0.08

Heritability estimates for stayability were low, and in agreement with Parker *et al.* (1959), Miller *et al.* (1967), Schaeffer (1975), Van Doormaal *et al.* (1986) and Snelling *et al.* (1995). Hudson & Van Vleck (1981) obtained estimates of 0.02, 0.04, 0.05, 0.05 and 0.05 at 36, 48, 60, 72 and 84 months respectively, in a Holstein herd.

Heritability estimates obtained for the different stayability levels were relatively constant across opportunity groups, except for the heritabilities of 0.10 and 0.11 for 48 and 84 months stayability. These estimates were slightly higher than for those of the rest of the stayability levels. Miller *et al.* (1967) also found heritabilities for herd life which were relatively constant across opportunity groups. However, Everett *et al.* (1976) and Hudson & Van Vleck (1981) showed that as the age at which stayability was measured increased from 36 to 72 months, so did the heritability for the different stayability levels.

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The heritability of 0.03 for calving success found in this study was low and is in agreement with those found in the literature. Meyer *et al.* (1990) obtained heritabilities of 0.08, 0.02 and 0.08 for calving success in Herefords, Angus and Zebu crosses respectively, while Mackinnon *et al.* (1990) reported an average heritability estimate for cow fertility of 0.11. The heritability of 0.08 for longevity was also low and corresponds with comparable estimates found in the literature (Parker *et al.*, 1959; Miller *et al.*, 1967; Hudson & Van Vleck, 1981).

Arguments against active selection for longevity include low heritabilities, an increase in generation interval, necessity to obtain survival information and automatic selection, as long-lived cows contribute more offspring to subsequent generations than short-lived cows (Parker *et al.*, 1959; Miller *et al.*, 1967; Nicholson *et al.*, 1978). However, Van Vleck's (Van Vleck, 1980) procedure for evaluating sires for stayability may reduce the waiting period for proof. Bakker *et al.* (1980) showed that stayability might be important in determining expected net profits from one conception.

2.3.4 Product moment correlations

Table 2.8 presents the product moment correlations between the various levels of stayabilities and calving success. These correlations were all low and varied from 0.01 (between 60 and 84 months) to 0.22 (between 48 and 84 months). No correlation of any genetic value could be found. There will be little to no improvement on any level of stayability when selection is applied on any other level. The same was found between calving success and the different stayability levels. This also emphasises the low heritabilities for these traits. These correlations differed from those found in the literature. Hudson & Van Vleck (1981) obtained correlations between stayability levels which varied between 0.72 and 1.00. A correlation of 1.00 was obtained for stayability between 60 and 72 months, 0.95 between 48 and 72 months, 0.76 between 36 and 60 months, 0.80 between 36 and 48 months, 0.70 between 36 and 72 months and 0.72 between 36 and 60 months.

In this study, if a cow was culled at 60 months, there were no further records for her. However, in Hudson & Van Vleck (1981) study, this cow would also received a zero for the 78 as well as for the 84 months level. Thus, in this study, a cow could receive a series of ones, but could only be awarded one zero during her lifetime, while a dam in Hudson & Van Vleck (1981) study could

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receive more than one zero. This could be the reason for the large differences between correlations found in the literature compared to this study.

Table 2.8 Product moment correlations between stayability levels and calving success

Traits	Stayability levels				Calving success
	48 months	60 months	72 months	84 months	
36 months stayability	0.22	0.13	0.09	0.14	0.14
48 months stayability		0.06	0.20	0.00	0.12
60 months stayability			0.19	0.01	0.04
72 months stayability				0.02	0.07
84 months stayability					0.20

2.3.5 Sire breeding values

Predicted breeding values (PBV) for the five best and worst sires for each trait are given in Table 2.9. There are no similarities in the rankings of sires between the different traits. This emphasises the low heritabilities of these traits and the low correlations between them. It confirms earlier suggestions that selection for these traits would result in little improvement.

Table 2.9 Predicted breeding values (PBV) of sires for stayability, longevity and calving success

36-mo stayability		48-mo stayability		60-mo stayability		72-mo stayability		84-mo stayability		Longevity		Calving Success	
ID NO	PBV	ID NO	PBV	ID NO	PBV	ID NO	PBV	ID NO	PBV	ID NO	PBV	ID NO	PBV
04113	0.123	06868	0.120	00433	0.081	04490	0.061	05224	0.155	04700	0.243	07834	0.152
05573	0.066	05224	0.101	05327	0.072	04569	0.049	04904	0.139	04490	0.222	03679	0.136
05894	0.064	00433	0.094	01600	0.058	03035	0.043	05964	0.118	00976	0.219	02434	0.133
03666	0.059	00252	0.085	07400	0.053	02863	0.035	06253	0.113	04569	0.206	05230	0.109
02439	0.055	03035	0.084	03035	0.051	00433	0.031	01069	0.099	02914	0.194	06958	0.092
00432	-0.084	05344	-0.108	06675	-0.068	01161	-0.034	01842	-0.096	00762	-0.152	07192	-0.113
08329	-0.084	08346	-0.110	00599	-0.070	06913	-0.043	03833	-0.108	00280	-0.155	02809	-0.115
08845	-0.087	00976	-0.126	05420	-0.074	04700	-0.048	04463	-0.116	00338	-0.166	05233	-0.115
05404	-0.088	08329	-0.161	02324	-0.086	05233	-0.053	05894	-0.134	02439	-0.186	04700	-0.120
03851	-0.108	03851	-0.191	03553	-0.108	04904	-0.058	04700	-0.253	00295	-0.191	06936	-0.126

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2.4 Conclusion

Stayability is the probability of surviving to a specific age, given the opportunity to reach that age. Provided that sufficient genetic variation exists, predictions of the genetic merit for stayability may allow selection of sires whose daughters are more likely to remain in the herd. It can also be useful in the selection of replacement heifers. As with any prediction of genetic merit, the decision of exactly how to use it, is determined by the individual. In this herd, animals were not only culled on poor reproduction performance but also on other unknown factors.

The heritabilities for and correlations between longevity, stayability and calving success as estimated from this data, appear to be of such a low magnitude that it seems unlikely to improve these traits through selection. It also indicates that the sire had little influence on his daughter's stayability, longevity and calving success. Thus, direct selection on the above-mentioned traits will result in limited genetic progress.

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CHAPTER 3
GENETIC PARAMETERS OF REPRODUCTIVE TRAITS IN A BEEF CATTLE HERD USING MULTITRAIT ANALYSIS

3.1 Introduction

Although reproduction is of critical importance to overall efficiency in the livestock industry, a completely satisfactory measure of reproduction has not been found. Reproduction is a complex process with many components. Several of these components have been used as measures of reproductive performance or as selection criteria. Some of these components are: calving interval (CI), calving rate, services per conception, age at first calving (AFC), days to calving and calving date (CD) (Meaker *et al.*, 1980; Bourdon & Brinks, 1983; Meyer *et al.,* 1990; Rege & Famula, 1993; Van der Merwe & Schoeman, 1995).

Animal geneticists are beginning to explore the possibility of separating components of the female "reproductive complex" into subsets that are both relatively easy to measure and have higher heritabilities. Calving interval has traditionally been the predominant measure of reproduction during the productive life of the animal, particularly in dairy cattle (Rege & Famula, 1993). However, in beef operations a relatively short breeding season is usually employed, so CI does not provide any additional information to CD and has lower repeatability and heritability (Bourdon & Brinks, 1983). Calving date was therefore suggested as the preferred criterion by these authors.

In South Africa, the National Beef Cattle Improvement Scheme assists farmers in the recording of important production information. The scheme gathers information from farmers and calculates specific values and indices that are used by the farmers to select their best animals. Age at first calving and calving interval are the criteria used in this scheme to evaluate reproductive performance (MacGregor, 1997). However, in South Africa, as in other countries, beef cattle are mostly mated during a limited breeding season. Bourdon & Brinks (1983), Marshall *et al.* (1990) and MacGregor (1995) have found CI to be a biased measure of reproductive performance due to its negative association with previous calving date (PCD). This results in cows calving early having the longest subsequent CI. Direct selection for a shorter CI could also result in indirect selection for later age at puberty, since cows with the shortest CI are often those who calve late in the previous calving season. For numerous reasons, Bourdon & Brinks (1983), Buddenberg *et al.* (1990), Lòpez de Torre & Brinks (1990), Marshall *et al.* (1990) and MacGregor (1995) suggested

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CD as the preferred reproduction measurement applicable to a restricted breeding season. These reasons include lower birth weights, reduced incidence of dystocia, higher weaning and yearling weights and higher reconception rates.

Reducing the age at first calving is one of only a few ways to improve lifetime efficiency in the beef cow (Van der Merwe & Schoeman, 1995). In general, beef heifers are managed to calve for the first time at three years of age. However, in many studies, first year mating of heifers was advocated (Fahmy *et al.*, 1971; Meaker *et al.*, 1980; Nunez-Dominguez *et al.*, 1991) and applied in the same herds, including the one under investigation. The advantage of mating heifers one year earlier lies in the potential increase in lifetime production of an extra calf (Meaker *et al.*, 1980). Most of the heritabilities for age at first calving found in the literature are low (Toelle & Robison 1985; Smith *et al.*, 1989; Frazier *et al.*, 1999) and indicate that age at first calving depends on nutritional and management levels. Most of these estimates were obtained by using unitrait analysis.

The objectives of this study were to obtain heritabilities for and genetic correlations between CI, CD and AFC in a multibreed beef cattle herd using multitrait analysis and also to evaluate the penalty effect for CD.

3.2 Materials and Methods

3.2.1 Animals and environment

Data used in this study were obtained from the multibreed beef cattle herd of the Johannesburg Metropolitan Council. The animals were kept on two farms on an intensive management system (Paterson, 1981; MacGregor, 1997). The herd was established in 1962 when several crossbreeding experiments were initiated involving Hereford, Angus, Simmentaler, Charolais, Sussex, Brahman, Bonsmara, Afrikaner and Holstein sires that were mainly used on Afrikaner, Hereford and Bonsmara cows. These crossbred groups were subsequently pooled. Over the years the breed genotype of the animals became complicated (Paterson, 1981; MacGregor, 1997) and 352 basic breed genotypes were identified from these crossbreeds.

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Females were mainly bred during two restricted breeding seasons of approximately three to four months each, although a few cows also calved out of season. They were normally bred, using AI, from September to December each year to calve from June to September the following year. Animals that did not conceive during this breeding period were bred for a second time from May to July. Figure 3.1 shows the average percentage of calves born per month during the 14-year period from 1979 to 1992. Most (92%) of the females calved from June to September, 2% calved from October to January, while 6% calved in the second calving season namely from February to May.

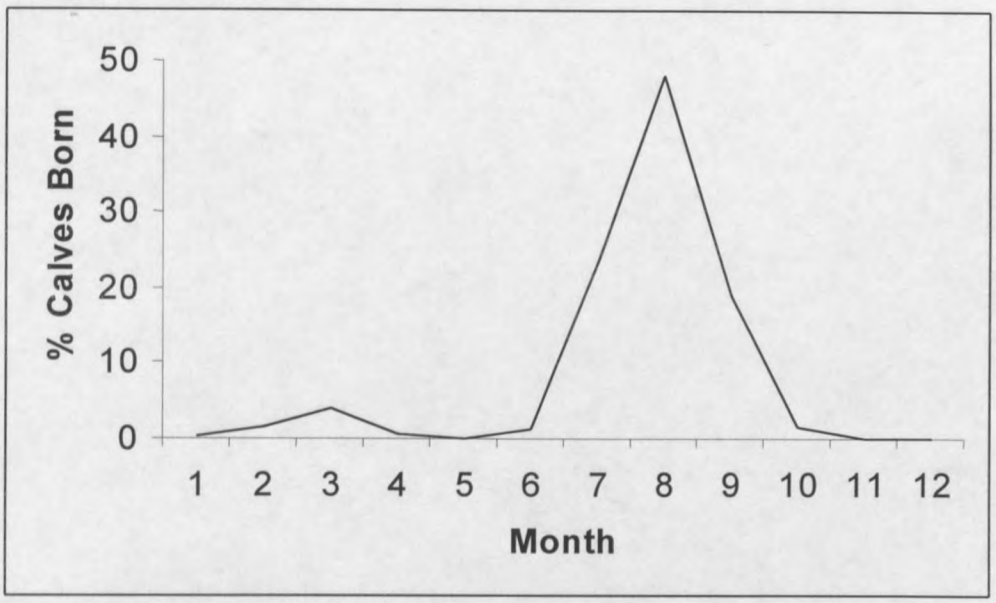

Figure 3.1 Percentage of calves born per month during the 14 year period of 1979 to 1992.

Eighty one percent of all females which gave birth in the second calving season, were first calving heifers. Heifers were bred to calf from June to October. The heifers which did not conceive during the first AI season, were rebred to calve from February to May the next year. Therefore, a number of heifers calved at two and a half years of age, from February to May. Due to the different breeding seasons and the fact that heifers had no calving interval record, all heifers were ignored in the operational model for calving date and calving date with a penalty score. Thus, only cow records were used in the analysis of calving interval, calving date and calving date with a penalty score. Month of calving varied from June to October.

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After incomplete records were removed, the data set contained 32 691 reproductive observations of 13 049 reproducing females between 1979 and 1992. There were 25 684 base animals in the pedigree file.

3.2.2 Trait description

Three reproductive traits were evaluated. They were calving interval, calving date and age at first calving. Calving interval was calculated as the interval in days between the present and previous calving dates. In this study CD was preferred to days to calving (DC), as the date of first joining for each female was unknown. In the literature DC (days to calving) was used by some authors (Meyer *et al.*, 1990). Days to calving is the number of days from first joining until birth. This trait is therefore basically the same as CD with the exception that DC includes the gestation period. Calving date was coded as the number of days from the onset of the calving season, taken from 1 June each year, until the dam calved. Calving date with a penalty score (CDP) was also evaluated. A penalty score for CD was given to those females which did not calve during a particular year. The cow having the highest calving date value in that specific year was identified and 21 days were added to her CD value. This value was assigned to all non-calvers for that particular year (Johnson & Bunter, 1996; MacGregor, 1997).

Figure 3.2 presents the frequency distribution for CD. Calving date varied between 20 and 138 days with a peak at 76 days. These were the dams that conceived during the first restricted breeding season and gave birth to a calf. The same applied to CDP, but as shown in Figure 3.3, a number of other peaks are observed. These peaks are the penalty values given to all non-calvers in each particular year. Table 3.1 presents the penalty value for the 14-year period from 1979 until 1992. The highest penalty value of 336 days was applied to all non-calvers in 1979 to 1981, while the lowest penalty value of 151 days was given to the non-calvers in 1982. In 1984 no non-calvers were recorded.

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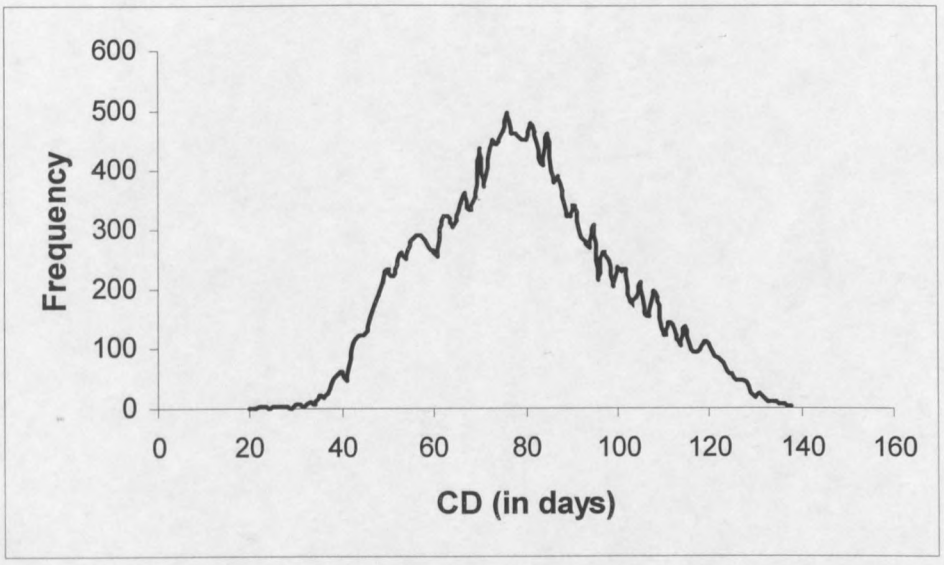

Figure 3.2 Frequency distributions for calving date (CD)

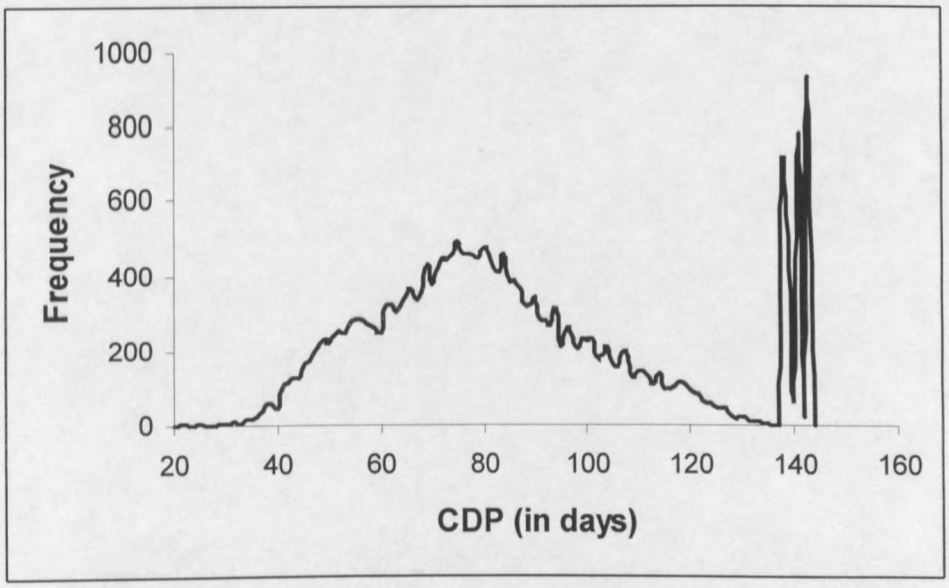

Figure 3.3 Frequency distributions for calving date with penalty scores (CDP)

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Table 3.1 Penalty values of non-calvers for each year

Year	Penalty value (in days)
1979	336
1980	336
1981	336
1982	151
1983	314
1984	-
1985	159
1986	292
1987	283
1988	298
1989	157
1990	334
1991	332
1992	332

Figure 3.4 presents the frequency distribution of CI and shows that the majority of dams recalved at approximately 369 days from their previous calving date.

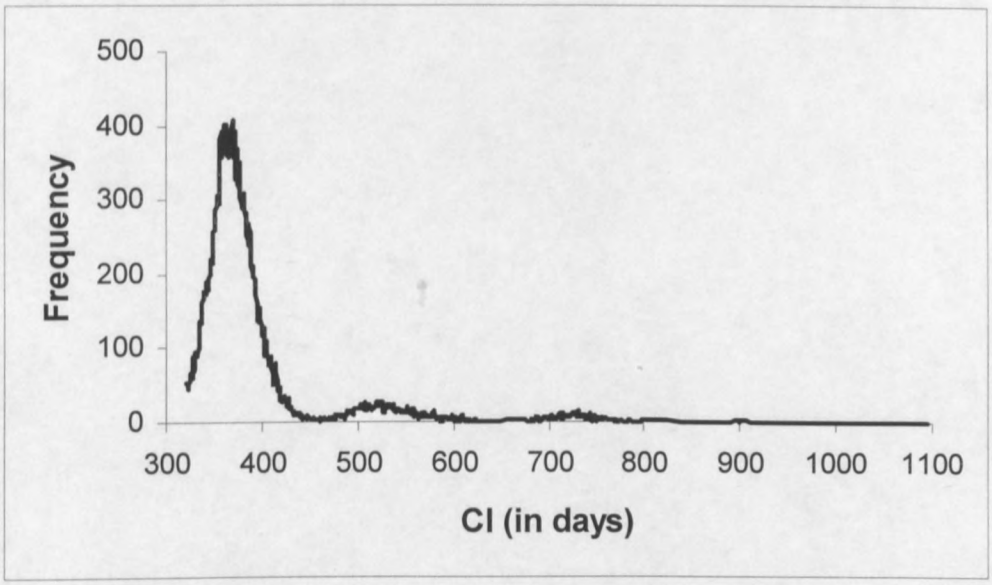

Figure 3.4 Frequency distributions for calving interval (CI)

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As shown by Figure 3.5, the majority of heifers calved for the first time at approximately 721 days of age. These are the yearling heifers that were bred in September to calve at two years of age in June. Those heifers that did not conceive during the first breeding season were rebred to calve at two and a half years of age in the January calving season. This is the reason for the smaller peak at approximately 923 days.

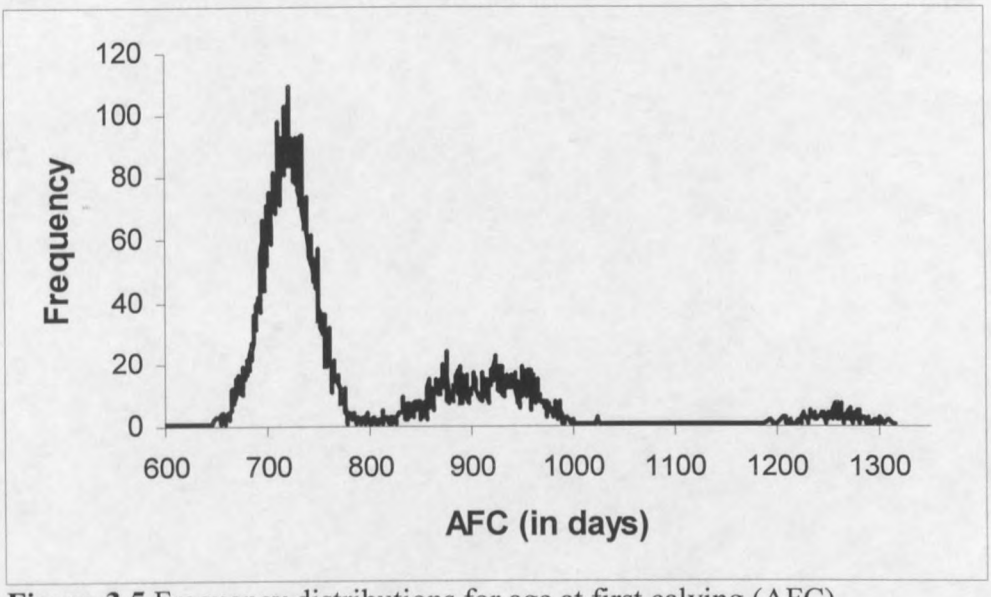

Figure 3.5 Frequency distributions for age at first calving (AFC)

3.2.3 Statistical methods

A restricted maximum likelihood procedure fitting a multitrait animal model (using the REML VCE 4.2.5 package of Groeneveld, 1998) was used to analyse the data. Traits were considered as traits of the dam. When considering the traits of the dam a repeatability model was fitted due to the repeatable nature of the traits. To determine the importance of possible non-genetic sources of variation on CI, CD, CDP and AFC, the following fixed effects were fitted into the initial model using the PROC GLM procedure of SAS (1993): the herd-year concatenation (HY) (46 levels), production year of the dam (14 levels) and genotype (352 levels), while the age of the cow was included as a covariate. Genotypes of the female were obtained from the files of Skrypzeck *et al.* (2000).

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The following model was used for analysis:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e},$$

where

$\mathbf{y}$ = vector of observations for the i^{th} trait,

$\mathbf{b}$ = vector of fixed effects for the i^{th} trait,

$\mathbf{a}$ = vector of random animal effects for the i^{th} trait,

$\mathbf{e}$ = vector of random residual effects for the i^{th} trait,

X and Z are incidence matrixes relating records of the i^{th} trait to fixed and random animal effects, respectively.

It is well known that CI has been found to be a biased measure of reproductive performance in a restricted breeding season due to its negative association with previous calving date (PCD). Therefore, a linear regression procedure of CI on CD, CD on PCD and CI on PCD was performed using the PROC REG procedure of SAS (1993).

3.3 Results and Discussion

3.3.1 Means and variation

Table 3.2 presents the number of records and general statistics for each of the traits.

Table 3.2 General statistics of reproductive traits, considered as traits of the dam

Traits	Total Records	Min. (Days)	Max. (Days)	Avg. (Days)	Std. Dev.
CI	22 799	322	1 095	390.73	71.72
CD	22 465	20	138	79.31	20.31
CDP	25 440	20	159	88.25	31.12
AFC	7 251	518	1 315	781.82	119.60

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The average calving interval of 390.7 days was in accordance with those found in the literature. Morris (1984), Meacham & Notter (1987) and Haile-Mariam & Kassa-Mersha (1994) found means for CI of 369, 378 and 441.7 with standard deviations of 20, 20 and 129.2 days, respectively. The higher standard deviation of 129.2 days obtained by Haile-Mariam & Kassa-Mersha (1994) could be due to the higher mean of CI obtained by them.

Calving date (CD) varied from 20 to 138 days with an average of 79.3 (± 20.31) days. For CDP the average was 88.3 (± 31.12) days. Larger mean values for both CD and CDP were reported in the literature. Meacham & Notter (1987) reported a mean value of 111 (± 22) days for CD, while a mean value of 110 days was reported by Morris (1984) and indicated that the majority of females calved fairly early in the calving season.

The data set for AFC comprised of 7 251 heifers. The average AFC was 781.8 (±119.60) days with a range of 518 to 1 315 days. It is clear that heifers in this herd were bred to calve at two years of age, while at least some of them which failed to calve early, were retained in the herd. An average for AFC of 1 271.4 days was reported by Haile-Mariam & Kassa-Mersha (1994).

3.3.2 Contribution of non-genetic sources

Table 3.3 presents the means, standard deviations, minimum and maximum values for dam age and month of calving. The average age of females in production was 5.3 years with a minimum and maximum value of 2 and 13 years, respectively. This indicates that females were culled early in their productive lives. Females in production calved between June and October with the majority calving during July each year.

Table 3.3 General statistics of the non-genetic effects

Variable	Mean	Std Dev	Minimum	Maximum
Dam age	5.30	2.78	2	13
Month of calving	7.64	0.95	6	10

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The following effects, as shown in Table 3.4 and 3.5, were significant (P = 0.001) for CD and CDP and were therefore included in the operational model: herd-year (HY), production year and genotype. In the initial model, genotype was not significant (P = 0.154) for CI, while HY was not significant (P = 0.085) for AFC. Therefore only HY and production year were included as fixed effects in the operational model for calving interval and production year and genotype for age at first calving. Dam age was considered as a co-variable but was not significant (P ≥ 0.01) for any of these traits.

Table 3.4 Analysis of variance of calving interval and calving date

Non-genetic sources	Calving Interval			Calving Date		
	df	Mean Square	Pr>F	df	Mean Square	Pr>F
HY	46	19 275.32	0.0001	44	49 061.51	0.0001
Production year	13	80 546.30	0.0001	13	2 195.49	0.0001
Genotype				351	404.22	0.0001
R^2		0.10			0.36	

The R^2 for CI, CD and CDP of 0.10, 0.36 and 0.21 are low and could be due to firstly, the composite nature of these female reproductive traits and secondly, to the influence of the environment on reproduction performance (Table 3.4 and 3.5). MacGregor (1997) also obtained low R^2 values for CI and CD of 0.45 and 0.17, respectively. The R^2 for AFC of 0.79 obtained in this study is, however, high and emphasises that the model for AFC fits the data fairly well (Table 3.5).

Table 3.5 Analysis of variance of calving date (with penalty scores) and age at first calving

Non-genetic sources	Calving date (penalty score)			Age at fist calving		
	df	Mean Square	Pr>F	df	Mean Square	Pr>F
HY	44	50 248.96	0.0001			
Production year	13	32 905.96	0.0001	13	527 241.69	0.0001
Genotype	348	893.51	0.0001	255	2 854.36	0.0001
R^2		0.21			0.79	

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Production year was significant (P<0.0001) for CI, CD, CDP and AFC. The shortest CI of 366.3 (± 1.40) days was recorded in 1992 and the longest, 444.1 (± 4.71) days, in 1979 (Table 3.6). The earliest mean CD of 76.3 (± 0.86) days, calculated from 1 June, was recorded in 1991 and the latest, 98.6 (± 3.34), in 1979. The difference between these years was 22.3 days. For CDP, the earliest mean of 75.3 (± 0.53) days was recorded in 1987 and the latest mean, 82.8 (± 2.23) days, in 1979. It seems that there was a slight improvement in all the traits from 1979 to 1991.

The herd-year (HY) concatenation had a significant (P = 0.0001) effect on CI, CD and CDP. HY also explained a large percentage of the variance, especially for CD and CDP. This clearly shows the influence of the environment on these traits. Table 3.6 presents the LS Means for each of the HY groups for CI, CD and CDP. For CI, the dams born in 1968 on farm one had the shortest CI of 362.9 (± 7.60) days while the dams born during 1987 on farm one had the longest CI of 404.1 (± 2.14) days. Females born during 1989 on farm one had the shortest CD of 57.8 (± 1.67) days while those born during 1968 on farm two had the longest CD of 95.2 (± 3.32) days.

Although genotype explains only a small fraction of the total variance (0.05, 0.07, 0.10 for CD, CDP and AFC) it was significant (P = 0.0001) for CD, CDP and AFC (Table 3.4 and 3.5). Because of the large number of genotypes (352, 349 and 256 for CD, CDP and AFC, respectively) the LS Means are not discussed in this paper.

3.3.3 Regressions

It is well known that CI is a biased measure of reproductive performance in a restricted breeding season due to its negative association with previous calving date (PCD), which results in cows calving early having the longest subsequent CI (Bourdon & Brinks, 1983; Marshall *et al.*, 1990; MacGregor, 1995). Direct selection for a shorter CI could therefore result in indirect selection for later calving, since cows with the shortest CI are often those who calve late in the previous calving season.

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Table 3.6 Least squares means and standard errors for calving interval (CI), calving date (CD), calving date with penalty scores (CDP) and age at first calving (AFC)

		CI	CD	CDP	AFC
Herd x Year	167	394.89 ± 14.668			
	168	362.88 ± 7.598	64.83 ± 3.256	58.79 ± 4.881	
	169	366.45 ± 5.691	67.70 ± 2.661	58.98 ± 4.104	
	170	371.71 ± 5.481	66.90 ± 2.340	60.11 ± 3.622	
	171	372.75 ± 4.113	66.37 ± 1.742	61.02 ± 2.693	
	172	380.19 ± 3.735	67.15 ± 1.633	61.05 ± 2.519	
	173	371.70 ± 2.629	66.39 ± 1.137	60.12 ± 1.748	
	174	370.65 ± 2.655	64.92 ± 1.137	62.32 ± 1.741	
	175	370.87 ± 2.551	67.45 ± 1.124	61.70 ± 1.721	
	176	371.60 ± 2.176	66.03 ± 0.970	65.73 ± 1.469	
	177	371.41 ± 1.798	65.46 ± 0.797	75.41 ± 1.152	
	178	373.91 ± 1.954	66.77 ± 0.868	69.37 ± 1.304	
	179	377.58 ± 1.659	66.09 ± 0.758	88.02 ± 1.049	
	180	375.29 ± 1.819	63.23 ± 0.850	70.07 ± 1.290	
	181	376.92 ± 2.030	64.15 ± 0.961	69.61 ± 1.458	
	182	375.28 ± 2.243	62.21 ± 1.109	69.23 ± 1.679	
	183	374.76 ± 1.911	64.03 ± 0.866	74.98 ± 1.297	
	184	373.64 ± 1.812	63.79 ± 0.847	73.65 ± 1.272	
	185	388.31 ± 2.003	66.83 ± 0.951	83.71 ± 1.386	
	186	383.88 ± 2.160	62.52 ± 0.964	72.58 ± 1.453	
	187	404.12 ± 2.143	62.35 ± 1.056	84.60 ± 1.514	
	188	402.87 ± 2.398	61.09 ± 1.211	86.49 ± 1.698	
	189	402.66 ± 3.136	57.79 ± 1.673	87.69 ± 2.314	
	267	375.16 ± 9.289			
	268	368.30 ± 6.024	95.23 ± 3.319	91.71 ± 4.877	
	269	370.81 ± 4.531	94.60 ± 2.236	86.77 ± 3.458	
	270	369.06 ± 3.988	92.66 ± 1.727	83.82 ± 2.663	
	271	370.45 ± 3.186	92.11 ± 1.370	88.16 ± 2.082	
	272	372.00 ± 4.129	90.86 ± 1.733	88.91 ± 2.631	
	273	372.07 ± 2.303	90.42 ± 1.011	85.32 ± 1.547	
	274	370.38 ± 1.850	89.87 ± 0.835	86.15 ± 1.268	
	275	370.87 ± 1.706	89.46 ± 0.778	87.10 ± 1.176	
	276	372.12 ± 1.627	91.16 ± 0.739	89.58 ± 1.121	
	277	376.39 ± 1.438	90.95 ± 0.661	96.46 ± 0.963	
	278	373.22 ± 1.783	89.91 ± 0.788	96.68 ± 1.161	
	279	383.25 ± 1.447	89.10 ± 0.667	104.76 ± 0.928	
	280	381.64 ± 1.436	90.75 ± 0.663	96.64 ± 1.002	
	281	376.22 ± 1.720	88.69 ± 0.770	93.57 ± 1.173	
	282	382.17 ± 1.495	87.88 ± 0.699	94.39 ± 1.050	
	283	390.58 ± 1.541	89.80 ± 0.721	96.21 ± 1.087	
	284	371.12 ± 1.559	87.17 ± 0.720	94.56 ± 1.086	
	285	381.13 ± 1.520	85.95 ± 0.708	95.40 ± 1.057	
	286	382.31 ± 1.887	85.30 ± 0.850	92.05 ± 1.291	
	287	382.30 ± 2.179	86.62 ± 0.967	98.14 ± 1.432	
	288	391.42 ± 2.249	89.43 ± 1.015	98.36 ± 1.534	
	289	400.48 ± 3.101	86.68 ± 1.434	96.40 ± 2.202	
Production year	79	444.07 ± 4.717	98.56 ± 3.342	82.79 ± 2.215	995.84 ± 6.950
	80	376.80 ± 1.438	97.93 ± 0.886	76.78 ± 0.607	847.74 ± 7.546
	81	374.76 ± 1.241	89.16 ± 0.819	78.45 ± 0.527	929.14 ± 3.739
	82	368.47 ± 1.256	93.90 ± 0.766	74.97 ± 0.530	756.00 ± 4.255
	83	373.44 ± 1.255	81.60 ± 0.837	77.19 ± 0.534	724.61 ± 4.518
	84	371.71 ± 1.239	80.86 ± 0.816	78.28 ± 0.525	727.90 ± 4.791
	85	369.04 ± 1.323	82.73 ± 0.855	77.97 ± 0.559	732.94 ± 4.543
	86	376.89 ± 1.332	78.62 ± 0.862	76.09 ± 0.560	723.73 ± 4.481
	87	391.19 ± 1.264	79.28 ± 0.817	75.25 ± 0.535	699.50 ± 4.316
	88	372.23 ± 1.328	77.12 ± 0.856	75.94 ± 0.560	717.20 ± 4.425
	89	368.55 ± 1.335	79.32 ± 0.853	76.23 ± 0.565	720.56 ± 4.316
	90	373.90 ± 1.326	78.60 ± 0.858	76.54 ± 0.568	712.44 ± 3.592
	91	367.67 ± 1.327	76.28 ± 0.863	75.82 ± 0.571	711.90 ± 3.972
	92	366.23 ± 1.399	76.51 ± 0.900	79.10 ± 0.599	718.33 ± 4.176

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The regression of CI on CD is presented in Figure 3.6. A regression coefficient of 0.58 (± 0.01) for CI on CD was obtained. This indicates that these two traits are positively correlated and if there were an improvement in the one there would also be an improvement in the other. Figure 3.7 presents the regression of CD on PCD. Calving date was delayed by 0.43 (± 0.01) days for each one day delay in previous calving date. MacGregor (1995) showed that CD was delayed by 0.18 (± 0.01) days for each one day delay in PCD. Both Bourdon & Brinks (1983) and Morris & Cullen (1988) found a 0.11 days delay in calving date for every one day delay in previous calving date (0.11 ± 0.02 and 0.11 ± 0.10 days, respectively).

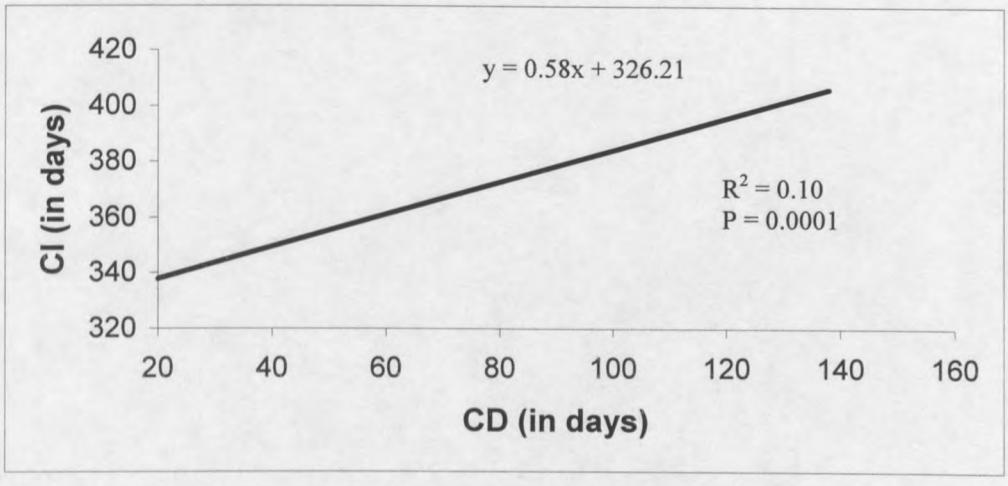

Figure 3.6 Regression of calving interval (CI) on calving date (CD)

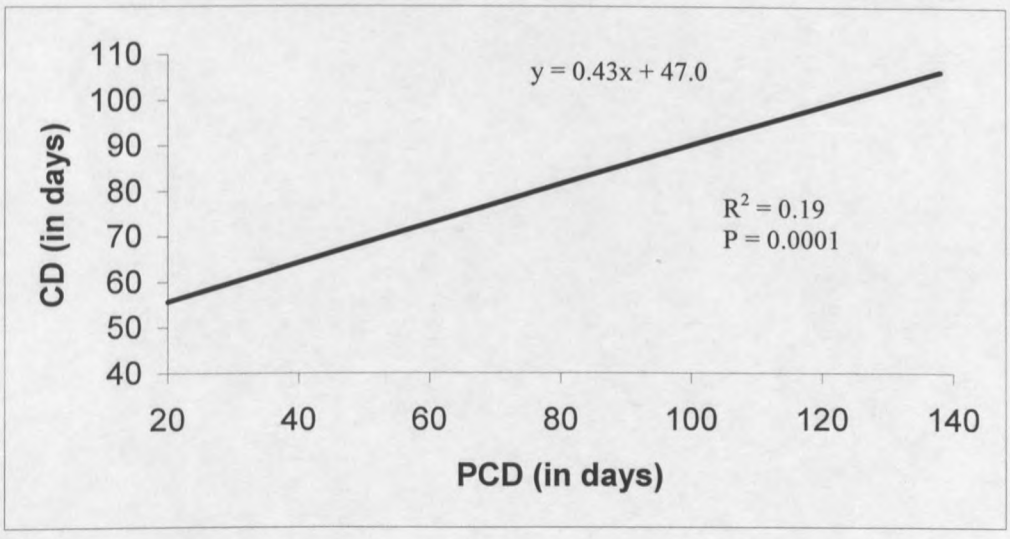

Figure 3.7 Regression of calving date (CD) on previous calving date (PCD)

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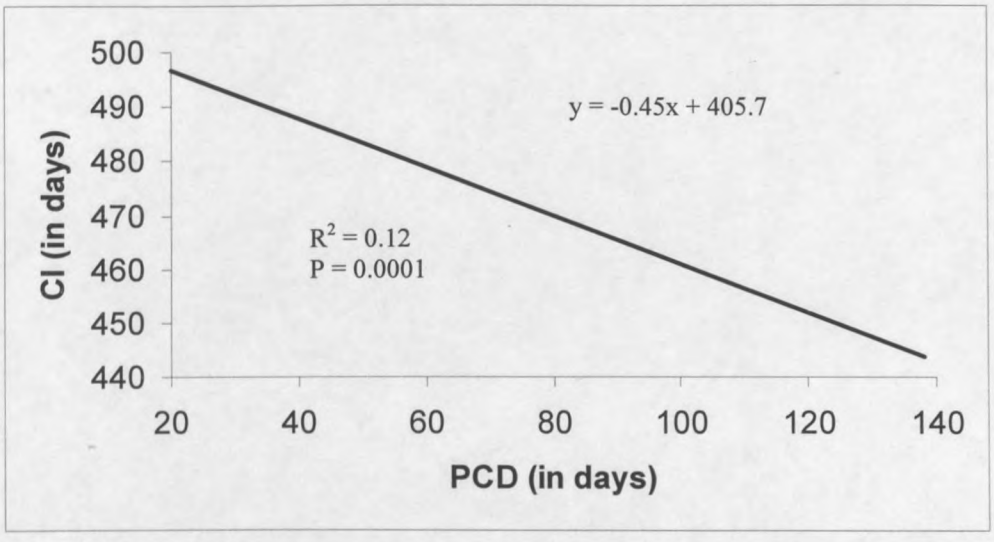

Figure 3.8 Regression of calving interval (CI) on previous calving date (PCD)

The regression of CI on PCD is presented in Figure 3.8. Calving interval was reduced by 0.45 (± 0.01) days for each one day delay in previous calving date, that is, cows that calved earliest the previous year had longer calving intervals the subsequent year than cows that calved later. The explanation of why early calving cows were unable to record shorter calving intervals when compared to late calvers is as follows: Early calving cows, having calved early, may have shown first oestrus before the introduction of the bulls or AI (started of the breeding season) and thereby were unable to record a shorter calving interval because they were unable to breed earlier. A poor selected calving season in which early calvers experience nutritional stress may also be a reason for early calvers not reconceiving as early as in the previous year, resulting in a longer subsequent calving interval. On the other hand, late calving cows may be induced into first oestrus through the effects of flush feeding or the introduction of the bulls (bull effect) or both, leading to earlier conception than the previous year, resulting in a shorter calving. If, however, the late calver did not show heat whilst the bulls were running with the cows and hence did not conceive, such a cow would be culled and excluded from the data.

In several studies (Bourdon & Brinks, 1983; Lishman *et al.*, 1984; Morris, 1984; Marshall *et al.*, 1990; Rege & Famula, 1993) a decrease in CI was found for each day delay in the previous calving date. Bourdon & Brinks (1983) found that calving interval was reduced by 0.86 (± 0.02)

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days for each one day delay in previous calving date. Likewise Morris (1984) found regression coefficients of 0.70 in Angus and 0.54 days in Hereford cattle.

The effect of previous calving date on calving interval is greater than the effect of previous calving date on present calving date. These findings would be expected since calving interval is essentially a function of previous calving date in that calving interval is calculated by subtracting the present calving date from the previous calving date. This suggests that CD is the preferable trait rather then CI in a restricted calving season.

3.3.4 Heritabilities and genetic correlations

Table 3.7 presents the heritabilities (h^2) for and genetic correlations (r_g) between CI, CD, CDP and AFC. Heritability estimates are presented on the diagonal (bold) while genetic correlations are above the diagonal. In general, heritabilities for reproductive traits are low. This is also the case in this study, with the exception of AFC.

Table 3.7 Heritabilities and genetic correlations for reproductive traits

	As traits of the dam			
Traits	CI	CD	CDP	AFC
CI	**0.01**	0.75	0.79	-0.03
CD		**0.04**	0.98	0.09
CDP			**0.06**	0.08
AFC				**0.40**

The heritability for CI of 0.01 corresponds with those found in the literature. Koots *et al.* (1994) reported a mean h^2 of 0.01 for CI (based on three estimates). López de Torre & Brinks (1990) also found a h^2 of 0.02 for CI. The h^2 estimates of 0.04 for CD also correspond with those found in the literature. Koots *et al.* (1994) reported a mean h^2 of 0.08 for CD (based on seven estimates), while Meacham & Notter (1987), López de Torre & Brinks (1990) and Rege & Famula (1993) obtained higher h^2 estimates of 0.16, 0.17 and 0.16, respectively.

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For a valid genetic evaluation of CD and variance component estimation, Notter (1988), Meyer *et al.* (1990), Ponzoni & Gifford (1994) and Johnson & Bunter (1996) emphasised the need to include all cows in the analysis, including cows that failed to calve during a restricted breeding season (non-calvers). Biased estimates are obtained if data of open cows are ignored as the results will ignore the most genetically inferior and, therefore, potentially the most informative animals (Notter, 1988). The heritability estimates obtained when open cows were excluded are expected to be biased downwards, thus suggesting that useful amounts of genetic variation for female fertility may exist (Notter, 1988). This requires that all non-calvers be assigned a penalty score value, which would allow their inclusion in the analysis. However, penalty values need to be calculated in such a way that they would not bias cows which did calve (MacGregor, 1997).

The procedure proposed by Notter (1988) and applied by both Buddenberg *et al.* (1990) and Meyer *et al.* (1990) used threshold theory to calculate penalty values of non-calvers. Ponzoni & Gifford (1994) applied the procedure of Meyer *et al.* (1990). They found that in calculating penalty values, the projected values fell within the calving period. They thus assigned all non-calvers the same value of 390 days. Johnson & Bunter (1996) found that this method produced a penalty value which was lower than 8% of all cows that calved in a specific year. Johnson & Bunter (1996) concluded that this result was unsatisfactory, as some calvers would be unfairly compared with non-calvers. Since cows are never in the same stage of their sexual cycle and since the breeding season may not start at the same time each year, a single penalty value for all non-calvers may be undesirable as it would fail to simulate the actual herd situation. If cows were not restricted to breeding during a restricted period, they would eventually mate and calve (MacGregor, 1997).

Three methods for assigning a predicted value to non-calvers were also investigated by Johnston & Bunter (1996). The first method (P360) assigned a value of 360 days to all non-calvers, and was the method described by Schneeberger *et al.* (1991). Johnston & Bunter (1996) showed that P360 did not produce a good predicted value to non-calvers, because there were cows that did calve with higher CD then 360 days. The other two methods identify a projected value that is assigned to each non-calver within a joining management group (i.e., the last calver within the group), and a constant number of days were added to this record to generate the projected value for all non-calvers. The two constants tested were plus 21 (P21) and 42 days (P42), respectively. MacGregor (1997) investigated two methods for assigning a predicted value to non-calvers. The first method involved establishing the relationship between present calving date and previous calving date by means of regression analysis. This he did by means of estimating the regression coefficient of

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present calving date on previous calving date, excluding all non-calvers that gave the following regression function:

- Present calving date = 55.41 + 0.07 × previous calving date (PCD)

In MacGregor's (1997) study, each non-calver was then assigned a present calving date value based on an own previous calving date. To apply the penalty value to ensure non-calvers received the longest calving days, 21 or 42 days were added to the value calculated from the regression. The second procedure was the P21 method that was described by Johnston & Bunter (1996). Johnston & Bunter (1996) and MacGregor (1997) suggested the P21 method, because this method of adding a fixed number of days to the last calving date of calvers to calculate a penalty-calving-date value for non-calvers, was successful in assigning a meaningful value to non-calvers. Therefore P21 was also used in this study.

The h^2 estimate for CDP of 0.06 is somewhat lower then the heritabilities found in the literature. assigned a penalty score for CD to all non-calvers and obtained a h^2 estimate for CD in first calvers of 0.39. The fact that a "relatively high" h^2 was found be Buddenberg *et al.* (1990) could be linked to the fact that his study was based on first calvers. The majority of h^2 estimates for these traits found in the literature were estimated using unitrait analyses and this could also be a reason for the higher h^2 found in the literature, especially for CDP, compared to this study. Although the heritabilities obtained for CD and CDP are both low, CDP's heritability was slightly higher than the heritability for CD. The heritability for CD would be expected to be biased downwards (Notter, 1988) because of the exclusion of all open cows. Therefore, a penalty value for CD must be given to all non-calvers. The penalty score effect may be a way to increase the heritability of CD and to ensure a less biased measurement for reproductive performance.

The genetic correlation between CD and CI of 0.75, suggests that selection for an earlier CD would decrease CI. The high positive genetic correlation between CI and CD confirm the positive regression of CI on CD. The same applies to the correlation between CI and CDP of 0.79. The high genetic correlation of 0.98 between CD and CDP, suggests that these two traits are basically the same trait.

The h^2 of 0.40 for AFC found in this study corresponds to other values found in the literature. Kassab (1995), Singh *et al.* (1996) and Magana & Segura (1997) obtained h^2 values for AFC of 0.46, 0.36 and 0.46, respectively. It therefore seems to be possible to change age at first calving

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through selection. However, Koots *et al.* (1994) reported a mean h^2 of 0.06 for AFC. Singh *et al.* (1996) found a r_g of 0.68 between AFC and CI. The r_g between AFC and CI, and AFC and CDP found in this study were very low and were of little genetic value.

Although the h^2 for both CI and CD were low, CD is the preferred trait rather than CI because of the high negative correlation between CI and PCD (previous calving date) and other disadvantages that CI has, as discussed by Bourdon & Brinks (1983), Buddenberg *et al.* (1990), Lòpez de Torre & Brinks (1990), Marshall *et al.* (1990) and MacGregor (1995). The heritabilities of CD and CDP and the genetic correlation between them obtained in this study, suggest that CD and CDP are the same trait and that CDP does not have any additional advantage.

Because of the repeatable nature of CI, CD and CDP, a repeatability model was fitted to these reproductive traits. Table 3.8 shows the repeatability estimate of the traits when traits were considered as traits of the dam.

Table 3.8 Repeatability of reproductive traits

Traits	Repeatability
Calving interval	0.07
Calving date	0.12
Calving date with penalty scores	0.13

The repeatabilities obtained for CI, CD and CDP of 0.07, 0.12 and 0.13 correspond with those found in the literature. For calving date, Harwin *et al.* (1969), Lesmeister *et al.* (1973), Baily *et al.* (1985) and Rege and Famula (1993) reported repeatabilities of 0.14, 0.10, 0.12 and 0.23, respectively. Lindley *et al.* (1958), Plasse *et al.* (1966), Schalles & Marlowe (1969) and Baily *et al.* (1985) obtained repeatability estimates for calving interval of 0.06, 0.03, 0.02 and –0.05, respectively. Repeatabilities for CD or CDP therefore seem to be higher than those for CI. These low repeatabilities were expected because of the low heritabilities that were obtained in this study. This suggests that if a dam calves early in a calving season it does not necessarily mean that she will calf early in the subsequent calving season, but that the environment plays a greater role in reproduction traits.

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3.4 Conclusion

In general, the heritabilities for all reproductive traits in the literature are low. The same appears to be the case in this investigation, with the exception of AFC where a high h^2 was estimated. However, selection for AFC would probably lead to animals that would be sexually mature at a younger age, but would most likely produce smaller calves.

Although the h^2 for both CI and CD were low, CD is the preferred trait rather than CI because of the high negative regression coefficient of CI on PCD. Heritabilities, genetic correlations and repeatabilities of CD and CDP obtained in this study suggest that CD and CDP are the same traits. Therefore, selection for CDP rather than for CD does not provide any additional advantage. No unfavourable genetic correlations have been identified in this analysis and it seems that CD is a suitable indicative trait for reproductive performance. The use of multitrait analyses in reproductive traits should become a more applied practice. It should be an essential part of analysing reproductive data, especially where selection indices for genetic improvement of reproduction become relevant.

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CHAPTER 4
GENERAL CONCLUSION

The rapid development of computer hardware over the last number of years has made the simultaneous development of more appropriate analytical software possible. These analytical techniques have resulted in more accurate prediction and estimation of genetic merit for reproductive traits. As such technology is utilised, producers will have the tools to apply direct selection on the economically important traits of female reproduction.

One of these analytical techniques that are of great interest is the development of multitrait analyses. In general, heritability estimates are more accurately predicted when a multitrait rather than unitrait model is used for the analysis. A second advantage of using multitrait analysis is that it is now possible to obtain genetic correlation estimates between traits. Therefore, the use of multitrait analyses in reproductive traits should become a more applied practice and should be an essential part of analysing reproductive data, especially where selection indices for genetic improvement of reproduction becomes relevant.

Despite this development, the software for the computation of threshold analyses is not as advanced. Heritability estimates for all categorical traits investigated in this study (calving success, longevity and stayability) were therefore estimated using a unitrait sire model. Heritability estimates obtained for calving success, longevity and stayability at 36, 48, 60, and 72 months were low and in agreement with those found in the literature. The low estimates obtained from this data appeared to be of such a low magnitude that it is unlikely that selection would lead to any improvement in these traits. This indicates that the sire had little influence on his daughter's stayability, longevity and calving success and that production, nutrition and the environment influences these categorical traits to a much greater extent.

Internationally, a few beef cattle breed associations have incorporated the so-called "stayability expected progeny difference" into national cattle evaluations. It is suggested that the reproductive lifespan of females through sire selection could be increased. The use of these expected progeny differences along with proper nutrition and management could promote favourable responses in the female reproductive performance.

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Estimates found in this study for calving interval, calving date and calving date with a penalty score were low. This agrees with the heritabilities found in the literature. The only exception with those found in the literature was the higher heritability for age at first calving. Due to the high heritability obtained in this study, selection for a decrease in age at first calving is possible in this herd. Selection for age at first calving would lead to animals that would be sexually mature at a younger age, but would most likely also produce smaller calves. Therefore, selection for age at first calving should be applied with discretion.

Although the h^2 for both calving interval and calving date were low, calving date is the preferred trait rather than calving interval because of the high negative regression coefficient of calving interval on previous calving date. Heritabilities, genetic correlations and repeatabilities of calving date and calving date with a penalty score obtained in this study suggest that calving date and calving date with a penalty score are the same trait. Therefore, selection for calving date with a penalty score rather than for calving date does not provide any additional advantage. No unfavourable genetic correlations have been identified in this analysis and it seems that calving date is a suitable trait for the improvement of reproductive performance.

When the low heritabilities obtained for most reproductive traits are considered against the importance of reproduction to the producer, a way should be devised which would make selection for female reproduction more effective. This could be possible by means of a selection index where all reproductive components could be included as a single criterion, including the male's reproductive components such as scrotum circumference. Further investigation in this regard is necessary.

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CHAPTER 5
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